

The discovery of a radula in a *Dentimargo* species and its taxonomic implications

Descubrimiento de la rádula en una especie de *Dentimargo* y sus implicaciones taxonómicas

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ABSTRACT

The discovery of a comb-like radula in specimens of *Dentimargo* cf. *aureocinctum* (Stearns, 1872) is recorded. The occurrence of such a radula in a presumed non-radulate genus suggests a very close relationship between the genus *Dentimargo* and the genus *Volvarina* Hinds, 1844. This matter invalidates the taxonomic organisation currently accepted within the Marginellinae, and especially that between the Tribes Marginellini and Prunini. The conchological differentiation of *Dentimargo* from the *Volvarina-Dentimargo* common stem is shown to have arisen before the loss of the radula, and this loss is considered to have little taxonomic value within the marginellid gastropods. Due to its high conchological similarity with the type species *D. dentifera* (Lamarck, 1803), *D.* cf. *aureocinctum* is conserved in the genus *Dentimargo*, which is provisionally considered as being composed both of radulate and of non-radulate species.

RESÚMEN

Se reseña el descubrimiento de una rádula en forma de peine en ejemplares de *Dentimargo* cf. *aureocinctum* (Stearns, 1872). La presencia de tal rádula en un género que se considera carecer de la misma indica una relación estrecha entre el género *Dentimargo* y el género *Volvarina* Hinds, 1844. Ello invalida la ordenación taxonómica actualmente aceptada entre los Marginellinae y particularmente entre las Tribus Marginellini y Prunini. Se muestra que la diferenciación conquiológica de *Dentimargo* a partir del estirpe común *Volvarina-Dentimargo* se ha producido antes de la pérdida de la rádula y que esta pérdida es de escaso valor taxonómico en gasterópodos marginéllidos. Considerando su gran semejanza conquiológica con la especie tipo *D. dentifera* (Lamarck, 1803), *D.* cf. *aureocinctum* se mantiene en el género *Dentimargo*, considerando en este tanto especies provistas de rádula cómo careciendo de la misma.

PALABRAS CLAVE: Marginellidae, *Dentimargo*, *Volvarina*, radula, clasificación supraespecífica, Caribe.

KEY WORDS: Marginellidae, *Dentimargo*, *Volvarina*, radula, supraspecific organisation, Caribbean.

INTRODUCTION

The generic name *Dentimargo* Cossmann, 1899, based on *Marginella dentifera* Lamarck, 1803 from the Mid-Eocene (Lutetian) of the Paris Basin, is com-

monly attributed to a series of marginellid species widely distributed in the Recent throughout the tropical and the subtropical zones from littoral to bathyal

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levels. The generic placement in *Dentimargo* is currently used for species with a tall spired, rather biconic, tiny shell, whitish shaded, generally not decorated or poorly banded, and presenting more or less developed labial denticles, the uppermost one being the largest.

Defined on this basis, the genus has been considered to be non-radulate because a radula could not be found in individual species checked respectively by BARNARD (1969), PONDER (1970) and COOVERT (1987). Commenting upon the record of "9 species known or strongly suspected to be non-radulate", COOVERT AND COOVERT (1995) considered the whole genus *Dentimargo* as non-radulate, analogous with the genera *Marginella* Lamarck, 1799 and *Glabella* Swainson, 1840, also claimed to be non-radulate and considered to be closely allied with *Dentimargo*. *Marginella* and *Glabella* are defined on the basis of having larger and thicker shells, generally not bearing a stronger upper labial denticle and exhibiting a richer axial, spiral or ocellate decoration.

COOVERT AND COOVERT (1995) grouped together *Dentimargo*, *Marginella*, *Glabella* and several *Dentimargo*-looking genera in the tribe Marginellini Fleming, 1828, considered to be distinct from the other Marginellinae tribes (Austroginellini COOVERT AND COOVERT 1995 and Prunini COOVERT AND COOVERT, 1995), principally by their rather biconic shell outline and by the claimed lack of a radula (the exception being the genus *Hyalina* Schumacher, 1817, which is said to have lost its radula but placed in the

Prunini because of its light cylindrical shell similar to that found in many species of *Volvarina* Hinds, 1844).

BOYER (2001: 160) underlined that "the presumed lack of a radula in the genus *Dentimargo* was controlled only about a restricted number of species and the type species *D. dentifera* Lamarck, 1803, a fossil species apparently represented from the Eocene to the Miocene, was naturally not checked for this character". BOYER (2001: 160) also explained that "numerous marginelliform species from the European Eocene... constitute a poorly differentiated *Volvarina-Dentimargo* complex, in which the "comb-like" radulae (typical of the radulate Prunini species) or their derived forms might be often represented". BOYER (2001: 160) observed that "the loss of the radula in a uniserial rachiglossan group is probably contracted easily, and this derived character seems to have been formed on several occasions in the radiation of the Marginellidae. From that, it is inferred that some *Dentimargo* lineages may have conserved their radula, like some *Volvarina* species may have lost theirs".

The present article is devoted to reporting on the discovery of a comb-like radula in a Caribbean species attributable to *Dentimargo*, and to the first general taxonomic inferences that can be issued from this discovery.

Abbreviations:

ERC: E. Rolán Collection.

FBC: Collection of the author.

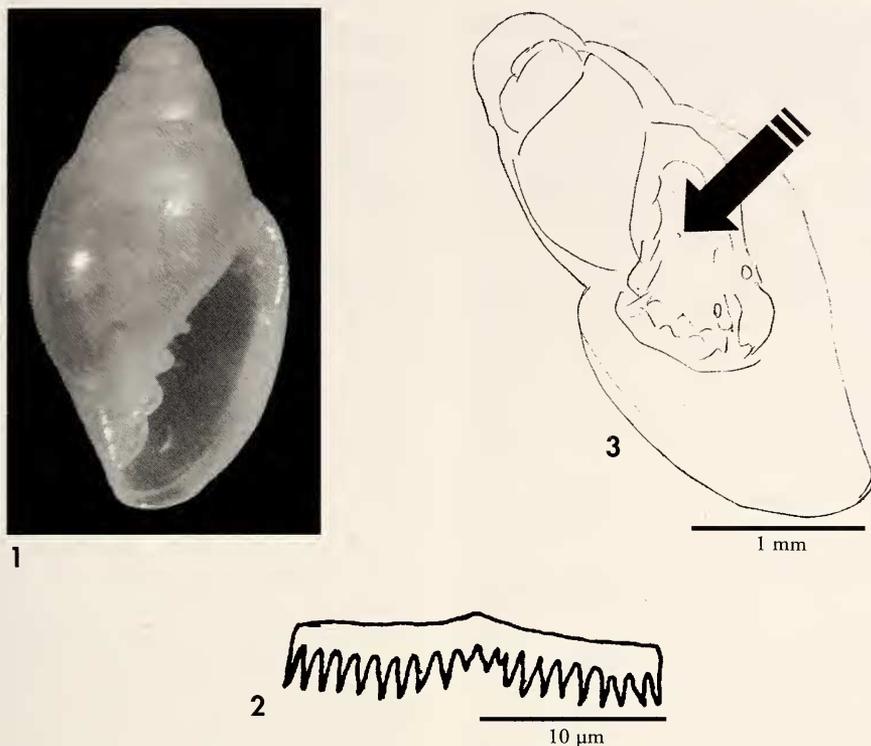
RESULTS

Family MARGINELLIDAE Fleming, 1828
Subfamily MARGINELLINAE Fleming, 1828
Genus *Dentimargo* Cossmann, 1899

Type species by original designation: *Marginella dentifera* Lamarck, 1803.

Dentimargo cf. *aureocinctum* (Stearns, 1872) (Figs. 1-3)

Marginella (*Glabella*) *aureocincta* Stearns, 1872: 22 [Type locality: Long Key, Florida].



Figures 1-3. *Dentimargo* cf. *aureocinctum* (Stearns, 1872). 1: shell from Puerto Morelos, Yucatan, height 3.50 mm; 2: radula plate from a juvenile specimen of 3.20 mm of shell length; 3: position of the radula seen by transparency (same specimen as in Figure 1).

Figuras 1-3. Dentimargo cf. aureocinctum (Stearns, 1872). 1: concha de Puerto Morelos, Yucatán, altura 3,50 mm; 2: diente radular de un juvenil de 3,20 mm de longitud de concha; 3: posición de la rádula vista por transparencia (mismo espécimen que la Figura 1).

Type material: Holotype (live collected) in the United States National Museum. Not examined.

Other material examined: Banded form. Florida: 4 adult specimens, 2 juvenile shells, screening in mud and grass, low tide, 2 feet, Tampa Bay (FBC); 2 adult specimens, hand dredged, 1-2 feet, St Andrews Bay (FBC).

White form. Florida: 2 adult shells, Crawl Key (FBC): the squatter of both shells as *D. cf. aureocinctum*. Yucatan: 3 adult (Figs. 1, 3) + 1 subadult + 1 juvenile specimens, 1 juvenile shell, Puerto Morelos (FBC, ex-ERC, lot 57 M 1994): all as *D. cf. aureocinctum*.

Description: STEARNS (1872: 22).

COOVERT (1987: 35-37) provided a good figure of the type-2 live animal of *D. aureocinctum* from southwest Florida (p. 36, fig. 3) and an extensive description of the animal external anatomy and chromatism. Two specimens were studied, with the adult and subadult specimens shell lengths being 3.88 mm and 4.36 mm respectively. The shell in dorsal view is shown to have a slender,

biconic profile, with 2 dark narrow spiral bands on the body whorl and 1 band on the spire whorls.

Radula: COOVERT (1987: 37) did not "attempt to extract radula from this species", but on the basis of the lack of radula displayed by PONDER (1970) in *Dentimargo cairoma* (Brookes, 1924) and of the apparent lack of radula in the Floridian *Dentimargo eburneola* (Conrad, 1834) checked by himself, COOVERT (1987: 37)

considered that it was "quite likely that *D. aureocincta* is also non-radulate".

In the frame of this study, a radula has been extracted from an adult (shell length= 3.50 mm), a subadult (shell length= 3.50 mm) and a juvenile (shell length= 3.20 mm) specimens originating from Yucatan (Puerto Morelos, FBC ex-ERC) and preserved in alcohol.

Adult specimen (Figs. 1, 3): radular extraction R-310, undetermined number of comb-like radular plates bearing 20-21 cusps. The radular ribbon is very small and sub-translucent (see the size of the ribbon at the tip of the black arrow in Figure 3) and it was very difficult to find. The length of this ribbon was 0,256 mm for a shell length of 32 mm. The ratio ribbon length/shell length is of about $1/125$.

Subadult specimen: radular extraction R-609. The radula was observed by transparency through the soft parts but was lost during the extraction process by low dissolving, due to its minute size. The radula was lying within a pouch situated at the distal tip of the extended proboscis. This pouch is interpreted as being the buccal pouch.

Juvenile specimen: radular extraction R-308, 54 comb-like radular plates of 20 μ m of width and bearing 20-21 cusps (Fig. 2).

Distribution: The species is said to range from Florida to Yucatan and the Greater Antilles, but the real identity of the tiny littoral *Dentimargo* species recorded from the Greater Antilles remains to be verified, due to the possible presence of several similar species in this area.

Remarks: VOKES AND VOKES (1983) record our species from Yucatan as "*Marginella (Dentimargo) aureocincta immaculata* Dall", and they picture (pl. 18, fig. 7) a shell of 2.9 mm length resembling our specimens closely (Fig. 1). This shell is however thicker, with a strong labrum bearing one produced upper denticle and 4 smaller ones positioned below the mid-part of the inner labrum. Our 3 adult specimens have lighter shells with a thinner labrum, one of them bearing a singular, pronounced upper labial denticle, the rest of the inner labrum being smooth (Fig. 1), whereas

the 2 other adult shells show 2 faintly distinct denticles below the pronounced upper one. For all the other features, our specimens perfectly match the one pictured in VOKES AND VOKES (1983).

The shells from Florida show the same general morphology and the same organisation of the columellar plaits and of the denticulated labrum (more commonly 3-4 tiny denticles below the produced upper one, occasionally only 2 tiny denticles or only the larger upper one), but they present a more slender outline with a more pointed spire and a narrower aperture. Most of the shells from Florida bear one honey-orange narrow spiral band on the spire whorls and 2 bands on the body whorl, on a light honey to deep white background colour, but some specimens or populations show a full-white shell (form *immaculata* Dall, 1890). Intergrades between the "banded form" and the "white form" are currently found. The squat form represented in Yucatan (the shell pictured in VOKES AND VOKES, 1983 and our lot from Puerto Morelos) is scarcely found off Florida (FBC: 1 white shell of "squat form" collected together with a white shell of the "slender form" at Crawl Key). No evident intergrades between the "squat form" and the "slender form" are known to us, so the squat-shelled populations are provisionally named as *D. cf. aureocinctum*.

The successful finding of a minute radula in *D. cf. aureocinctum* has occurred 3 times out of the 3 checkings made in the limited material at hand. Examined by transparency within the alcohol-preserved animal, the radula is verified to be situated at the tip of the proboscis, as well when the proboscis is in extended position (observation in the subadult specimen) than when the proboscis is in retracted position (observation in an adult specimen, Fig. 3). In 2 out of the 3 tentatives, the radular extraction was performed with success and the same minute comb-like radula was documented (Fig. 2). These data allow to leave out the hypothesis giving these radulae as remains of digested preys. The data at hand confirm the radulate status of the species and the belonging of this radula to the "*Volvarina-Prunum* comb-like pattern".

DISCUSSION

The centrally depressed outline of the plates and the smallest cusps placed in median position are unusual features compared to the comb-like radulae known to us from the *Volvarina-Prunum* series (COOVERT AND COOVERT, 1990), which have generally a straight or faintly convex anterior cusped edge, together with uniformly distributed sub-equal small cusps, or sub-equal small cusps with a larger central cusp, or series of sub-equal small cusps separated by isolated larger cusps. However the number of plates like the number and the shape of the cusps in *D. cf. aureocinctum* are similar to the pattern found in numerous *Volvarina-Prunum* species. In summary, the radula of *D. cf. aureocinctum* is coherent with the range of variability found in the *Volvarina-Prunum* series, more than with the radular patterns found in the *Serrata* series (high number of subequal cusps) or in the *Mesoginella* complex (triangular anterior cusped edge, with a large central cusp and few laterals).

Despite the minute size of the radula found in *D. cf. aureocinctum*, there is no reason, in the present state, to consider it as vestigial. For instance, a minute radula with single, narrow plates is also found in the marginellid genus *Hydroginella* known as ectoparasit feeding at night on sleeping fishes (BOUCHET, 1989; JOHNSON, JOHNSON AND JAZWINSKI, 1995). As assumed by JOHNSON ET AL. (1995) about the similar case found in *Colubraria*, such minute plates seem to work as cutting out the fish's skin, as precondition of a feeding process by suction of the fish's blood. This point allows to infer that the comb-like radula of *D. cf. aureocinctum* may as well be functional despite its minute size. Such a minute size of the radula may also be considered, from an evolutionary point of view, as an intergrading stage towards the loss of the radula.

Due to its biconical shell outline, its produced upper labial denticle and its faint lower denticles, *D. cf. aureocinctum*

is demonstrated to be morphologically very similar to the fossil type species *D. dentifera*. For this reason its placement in *Dentimargo sensu stricto* is conservatively proposed as the most parsimonious solution.

However, it must be underlined that other *Dentimargo*-shelled species closely matching with *D. dentifera* [like for instance the New Zealand *D. cairoma* (Brookes, 1924) studied by PONDER (1970), the Floridian *D. eburneola* (Conrad, 1834) checked by COOVERT (1987) or the Mascarene *D. pumila* (Redfield, 1870) checked by the author] really do seem to be devoid of a radula. The matter signifies that the occurrence of the radula is represented as a heterogeneous character within the *Dentimargo* series and that it cannot be used as a diagnosis feature for the genus. In other words, *Dentimargo* is provisionally considered as being composed both of radulate and of non-radulate species.

As a direct consequence, the loss of the radula is likely to be of low discriminating value in marginellid gastropods. Besides, it must be emphasized that the loss of the radula may have arisen independently in different lineages. This point leads to a reconsideration not only about the phyletic unity of *Dentimargo*, but also about the degree of relationship occurring between *Dentimargo* and the supposed non-radulate genera *Marginella* and *Glabella*.

On the other hand, the *Volvarina*-patterned radula found in *D. cf. aureocinctum* proves that the conchological distinction between *Dentimargo* and *Volvarina* (not well marked in the Eocene, but more clearly displayed in the Recent) took place before the loss of the radula, at least in one of the *Dentimargo* lineages. Secondly, the radula found in *D. cf. aureocinctum* suggests a very close relationship between *Volvarina* and *Dentimargo*, without care about the order of disbranching from a comb-like radulate ancestor.

The discovery of a radula in the supposed non-radulate group *Dentimargo* and the inferred phyletic proximity between *Dentimargo* and *Volvarina* lead

to the assumption that the generic diagnosis and the supraspecific distinctions currently accepted within the Marginellinae remain mainly non-operative, in particular about the separation between the Prunini and the Marginellini, and about their respective composition.

The matter requires a general reassessment of the organisation of the Marginellinae, based on a new documentation provided by extensive comparisons concerning the morphologic disparity occurring in fossil and Recent shell material, and by correlative researches about the radula. Additional comparisons concerning internal anatomy and DNA patterns may prove to be more decisive for a clear reconsti-

tution of the disbranchings within the subfamily.

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